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On the relevance of the character "absence of epicoracoid horns" in the systematics of anurans

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Several authors consider the character "absence of epicoracoid horns" a synapomorphy of the group that includes the anuran families Dendrobatidae, Hyperoliidae, Microhylidae, Ranidae and Rhacophoridae (i.e., Ranoidea). However, others have suggested that this condition is plesiomorphic (i.e., epicoracoid horns are absent in several non-Ranoidea frogs) and that Ranoidea frogs possess epicoracoid horns. The pectoral girdles of several Ranoidea and non-Ranoidea frogs were sectioned histologically, and all had epicoracoid horns. The presence of epicoracoid horns in Ranoidea frogs suggests the character "absence of epicoracoid horns" is not a synapomorphy of this group.

INTRODUCTION

Several authors (GRIFFITHS, 1963, KLUGE & FARRIS, 1969; LYNCH, 1973; DUELLMAN & TRUEB, 1985) hypothesized that the families Dendrobatidae, Hyperoliidae, Microhylidae, Ranidae and Rhacophoridae form a monophyletic group supported by the synapomorphy "absence of epicoracoid horns" (i.e., posteriorly directed processes of the epicoracoid cartilages. GRIFFITHS, 1957, 1960*a-b*, 1963)

The hypothesis that the character "absence of epicoracoid horns" is a synapomorphy of Ranoidea is questionable, first, because the absence of epicoracoid horns (MCDIARMID, 1971, TRUEB, 1973, RUIZ-CARRANZA & HERNANDEZ-CAMACHO, 1976, GRANDISON, 1981, LYNCH & RUIZ-CARRANZA, 1982, MYERS & FORD, 1986, TYSON, 1987) in several non-Ranoidea frogs (i.e., *Atelopus*, *Atopophrynus*, *Brachycephalus*, *Dendrophryniscus*, *Didymampus syoestedti*, *Melanophryniscus*, *Oreophrynella*, *Osornophryne*, *Rhinophrynus dorsalis*) suggests this character is plesiomorphic at the level of Ranoidea, and second, because it has been suggested (KAPLAN, 1994) that Ranoidea frogs have epicoracoid horns that are fused, indistinguishably, to the sternum. However, the absence of epicoracoid horns in non-Ranoidea frogs and their

presence in Ranoidea frogs is controversial (KAPLAN, 1994; TYSON, 1987) and requires confirmation through detailed (i.e., histological) morphological examinations.

Herein, the girdles of several species of Ranoidea and non-Ranoidea frogs are examined through histological sectioning in order to assess the distribution of the character "absence of epicoracoid horns" in frogs. The hypothesis that the character "absence of epicoracoid horns" is a synapomorphy of Ranoidea is evaluated in light of the new morphological observations.

MATERIALS AND METHODS

The medial portion of the ventral elements (omosternum, clavicles, procoracoids, epicoracoids, coracoids, sternum) of the pectoral girdle of individuals at different developmental stages (GOSNER, 1960, in parentheses) of the following species was sectioned (App. 1). Ranidae: *Rana blairi* (44, adult); Dendrobatidae: *Colostethus subpunctatus* (44, 46, adult); Microhylidae: *Gastrophryne carolinensis* (43, 44, adult), Hyperoliidae. *Kassina senegalensis* (44, adult), Rhacophoridae: *Rhacophorus moltrechti* (44, adult); Bufonidae *Oreophrynella quelchii* (adult), *Melanophryniscus stelzneri* (adult) and *Dendrophryniscus brevipollicatus* (adult); and Brachycephalidae, *Brachycephalus ephippium* (adult). Abbreviations for institutions are as follow: ICN, Instituto de Ciencias Naturales, Universidad Nacional de Colombia; UMMZ, University of Michigan Museum of Zoology.

The medial portion of the ventral elements of the pectoral girdles of adults and juveniles was excised by cutting through the right and left procoracoid cartilages, clavicles, coracoid bones, and around the omosternum and sternum, when present, the medial portion of the ventral elements of the pectoral girdles was removed, decalcified (Cal-Ex II, Fisher Scientific), and sectioned transversely from the anterior tip of the omosternum to the posterior tip of the sternum, *Brachycephalus ephippium* was sectioned from the tip of the snout to the posterior part of the girdle. Tissues were embedded in paraffin (WESSNER, 1960), sectioned (15 μm), and stained with hematoxylin eosin. Histological and osteological terminologies follow those of FAWCETT (1986) and DE VILLIERS (1924), respectively.

Herein, I consider the epicoracoid horns to be parts of the epicoracoid cartilages that extend posteriorly to the posteromedial part of the coracoid.

RESULTS

Descriptions of the zonosternal articulation (fig. 1) of non Ranoidea and Ranoidea frogs.

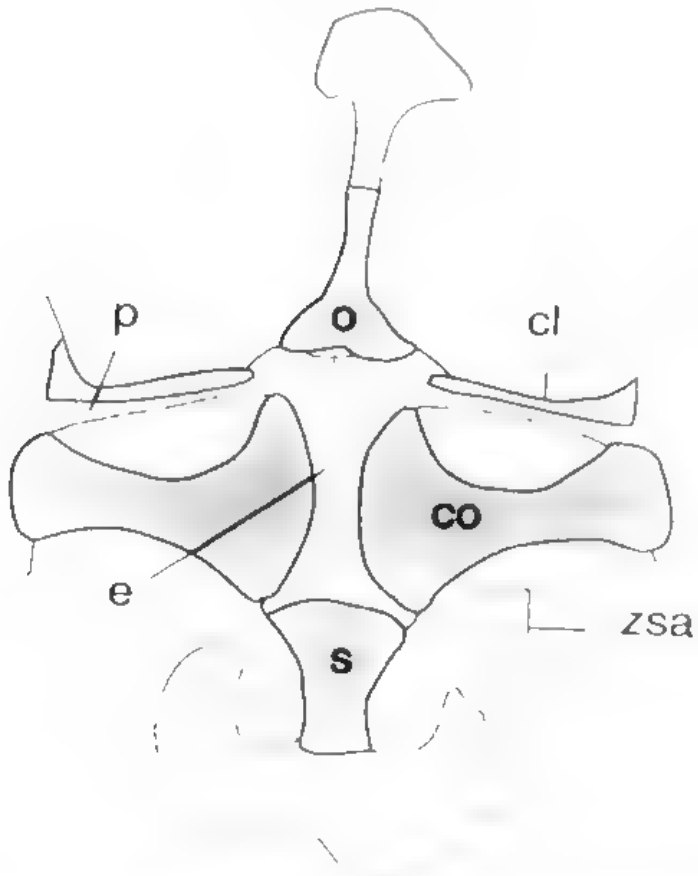

Fig 1 Ventral view of the pectoral girdle of *Rana blairi*, showing the interaction between the right and left halves as the meet medially cl, clavicle, co, coracoid, e, epicoracoid, o, omosternum, p, procoracoid, s, sternum, zsa, zonosternal articulation. Grey, bone, clear, cartilage.

NON-RANOIDEA FROGS

In *Dendrophryniscus brevipollicatus*, *Melanophryniscus stelzneri* and *Oreophrynella quelchii*, each epicoracoid cartilage bears a tapered, divergent cartilaginous process that extends posteriorly from the coracoids (fig 4A-C) In *Brachycephalus ephippium*, the posterior processes of the epicoracoids are short, thin, not diverging from, and firmly attached (but not indistinguishably fused) to, each other (fig. 4D).

In *Oreophrynella quelchii*, the *m. sternoepicoracoideus* does not insert on the posterior terminus of the posterior processes of the epicoracoids. In *Melanophryniscus stelzneri*, a laterally directed ligament inserts on the posterior terminus of each process, the *m. sternoepicoracoideus* does not insert on the ligaments. In *Dendrophryniscus brevipollicatus*, a posteriorly directed ligament inserts on the posterior terminus of each process, these ligaments are long and extend parallel to the lateral margins of the sternum, the *m. sternoepicoracoideus* inserts on the posterior ends of these ligaments. In *Brachycephalus ephippium* two short, wide

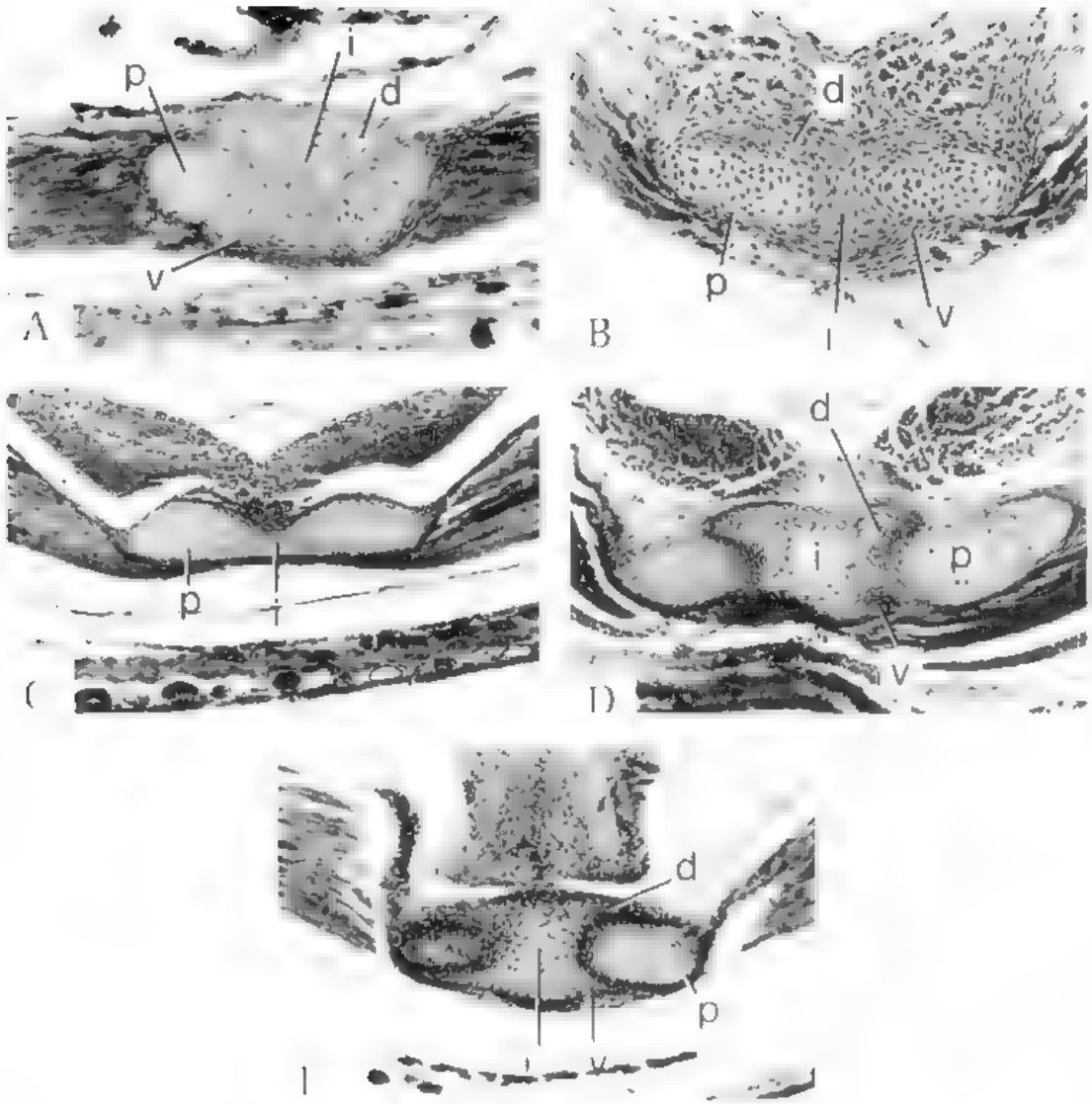

Fig. 2. – Transverse sections of the zonosternal articulation of the premetamorphic individuals (developmental stage in parenthesis) of the following species (A) *Colostethus subpunctatus* (46), (B) *Gastrophryne carolinensis* (43), (C) *Kassina senegalensis* (44), (D) *Rana blairi* (44), (E) *Rhacophorus moltrechti* (44). d, dorsal sternal blade, i, sternal isthmus, p, posterior process of the epicoracoids, v ventral sternal blade

slips of the *m. sternoepicoracoideus* insert on the posterior termini of the posterior processes of the epicoracoids; no ligament mediates the insertion of the *m. sternoepicoracoideus* on the posterior processes of the epicoracoids.

As seen in sectional view, in *Dendrophryniscus brevipollicatus*, *Melanophryniscus stelzneri* and *Oreophrynella quelchii*, each lateral margin of the isthmus of the sternum bears a lateral

groove formed by dorsal and ventral blades (fig. 4A-C). In *Brachycephalus ephippium*, the sternum is absent.

In *Dendrophryniscus brevipollicatus*, *Melanophryniscus stelzneri* and *Oreophrynella quelchii*, the posterior processes of the epicoracoids are housed in the sternal grooves (fig. 4A-C). In *D. brevipollicatus*, *M. stelzneri* and *O. quelchii*, the anterior portion of the posterior processes of the epicoracoids has its dorsal, medial and ventral surfaces separated from the sternum by a gap. In *D. brevipollicatus* and *M. stelzneri*, a thick ligament surrounds and attaches the lateral surfaces of the posterior processes of the epicoracoids to the dorsal and ventral sternal blades; posteriorly, the posterior processes of the epicoracoids run parallel to the lateral margins of the sternum for a short distance; in *M. stelzneri*, the posterior ends of the processes are firmly attached to the sternum by ligaments. In *O. quelchii*, the posterior parts of the posterior processes of the epicoracoids are fused to the sternum.

Ranoidea frogs

In premetamorphic individuals of *Colostethus subpunctatus*, *Gastrophryne carolinensis*, *Kassina senegalensis*, *Rana blairi* and *Rhacophorus moltrechti*, each epicoracoid cartilage bears a blunt, tapered, ovoid (in transverse section), divergent cartilaginous process that extends posteriorly from the coracoids (fig. 2A-E), the *m. sternoepicoracoideus* (i.e., epicoracoid horn muscle: Griffiths, 1963) does not insert on the posterior terminus of the process. As seen in sectional view, each lateral margin of the isthmus of the sternum bears a lateral groove formed by dorsal and ventral blades; the posterior processes of the epicoracoids are housed in the sternal grooves and fused to the sternum.

In adult individuals of *Colostethus subpunctatus*, *Rana blairi*, and *Rhacophorus moltrechti*, the medial surfaces of the posterior processes of the epicoracoids are separated from the sternum by a gap (fig. 3A-C). In *R. blairi* and *R. moltrechti*, the posterior tips of the posterior processes of the epicoracoids are mostly eroded; thus, the posterior parts of the sternal grooves are empty or contain few fragments of the processes. In *R. moltrechti*, the sternal isthmus is thinner (in transverse section) than the posterior processes of the epicoracoids. In *Gastrophryne carolinensis* and *Kassina senegalensis*, the posterior processes of the epicoracoids are indistinguishably fused to the sternum. The ventral sternal blade is absent in *Colostethus subpunctatus*.

Discussion

All the species of frogs examined exhibit two processes of the epicoracoids that extend posteriorly to the coracoids. In all Ranoidea frogs examined, the posterior processes of the epicoracoids are evident in premetamorphic stages, however, these processes in adults can be partly eroded (e.g., *Rana blairi*, *Rhacophorus moltrechti*) or indistinguishably fused to the sternum (e.g., *Gastrophryne carolinensis* and *Kassina senegalensis*). In all non-Ranoidea frogs examined (i.e., *Brachycephalus ephippium*, *Dendrophryniscus brevipollicatus*, *Melanophryniscus-*

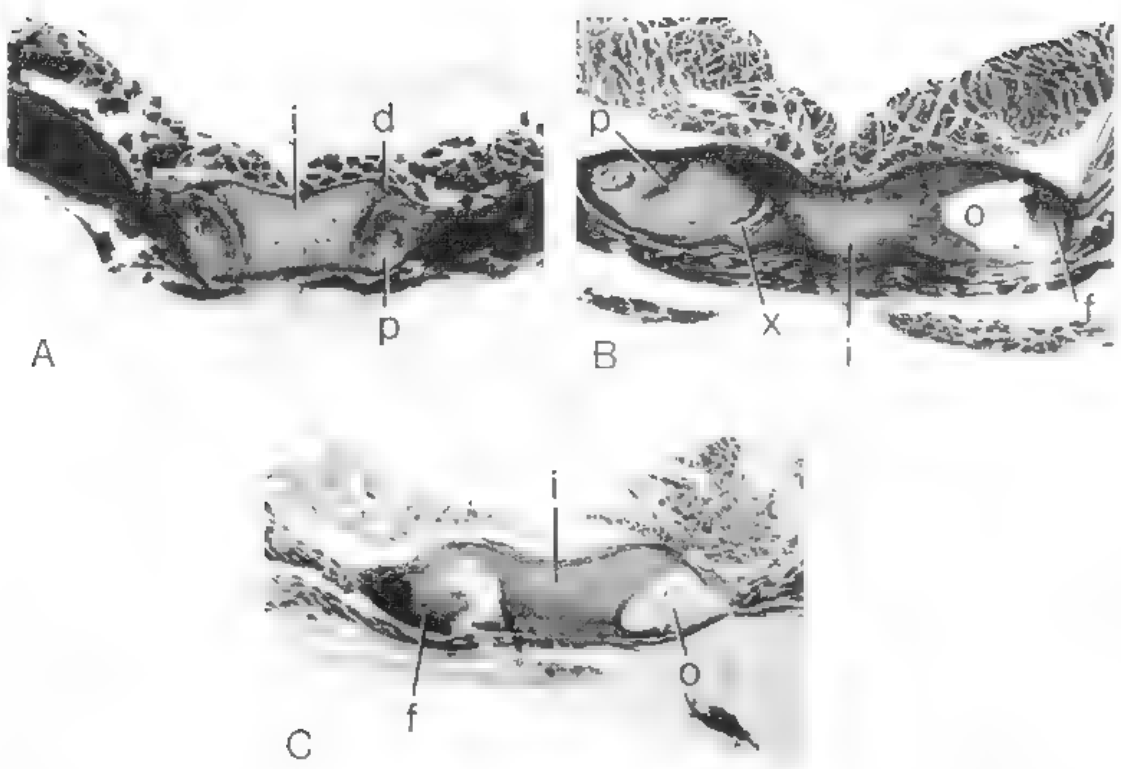

Fig. 3. Transverse sections of the zonosternal articulation of adult individuals of the following species (A) *Colostethus subpunctatus*; (B) *Rana blairi*; (C) *Rhacophorus moltrechti*. d, dorsal sternal blade; i, sternal isthmus; f, fragment of one of the posterior processes of the epicoracoids; o, empty sternal groove; p, posterior process of the epicoracoid; x, gap.

cus stelzneri, *Oreophrynella quelchii*), the posterior processes of the epicoracoids are evident in adults.

The posterior processes of the epicoracoids of all the species here studied must be considered epicoracoid horns because, like the horns of arciferal frogs (e.g., *Ascaphus*, *Bufo*, GRIFFITHS, 1963), they are posterior extensions of the epicoracoid cartilages and show the same topographic relation to other body parts (e.g., they are housed in sternal grooves).

This study challenges previous reports (MCDIARMID, 1971; TRUEB, 1973, TYSON, 1987) that epicoracoid horns are absent in *Brachycephalus*, *Dendrophryniscus*, *Melanophryniscus* and *Oreophrynella*. The presence of epicoracoid horns in these taxa suggests that all non-Ranoidea frogs have epicoracoid horns (however, note that the presence of epicoracoid horns in taxa such as *Osornophryne*, *Geobatrachus*, *Atopophrynus*, *Didynamipus* and *Rhinophrynus dorsalis* still needs to be demonstrated), and therefore, that the character "absence of epicoracoid horns" is not pleisiomorphic at the level of Ranoidea. However, the character "absence of epicoracoid horns" is invalid as a synapomorphy of Ranoidea because, as this study suggests, all Ranoidea frogs have epicoracoid horns (note that the monophyly of

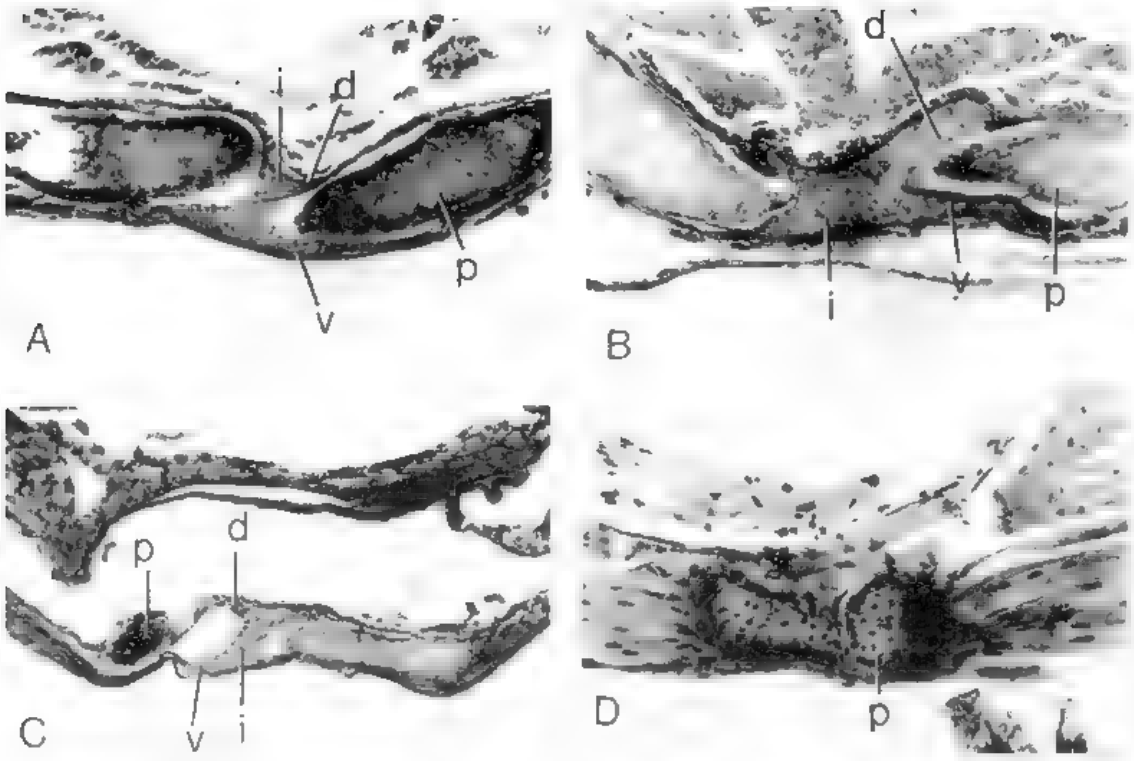

Fig 4 - Transverse sections of the zonosternal articulation of adult individuals of the following species. (A) *Dendrophryniscus brevipollicatus*, (B) *Melanophryniscus stelzneri*, (C) *Oreophrynella quelchii*, (D) *Brachycephalus ephippium* d, dorsal sternal blade; i, sternal isthmus, p, posterior process of the epicoracoid, v, ventral sternal blade.

Ranoidea is still supported by the characters "epicoracoid cartilages completely fused" and "medial end of the coracoids wider than lateral end": FORD & CANNATELLA, 1993)

I found considerable morphological variation in the epicoracoid horns of frogs: these can be fused or free from the sternum, short or long, rounded or thread-like, extending parallel to the lateral edge of the sternum or not. The systematic value of these characters, and the independence from each other, is currently unknown.

RESUMEN

Varios autores consideran que el caracter "ausencia de cuernos epicoracoidales" es una sinapomorfia del grupo (Ranoidea) que incluye a las familias Dendrobatidae, Hyperoliidae, Microhylidae, Ranidae y Rhacophoridae. Sin embargo, se ha sugerido que esta condición es plesiomorfica (esta presente en varios anuros que no son Ranoidea) y que los anuros Ranoidea tienen cuernos epicoracoidales. Las cinturas pectorales de varios anuros Ranoidea y no Ranoidea fueron seccionados histologicamente y se encontro que todos tienen cuernos

epicoracoidales. La presencia de cuernos epicoracoidales en anuros Ranoidea sugiere que el caracter "ausencia de cuernos epicoracoidales" no es una sinapomorfia de este grupo.

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APPENDIX 1
SPECIMENS EXAMINED

Rana blairi (UMMZ 224284-5); *Colostethus subpunctatus* (ICN 15822, 23308; UMMZ 224288); *Gastrophryne carolinensis* (UMMZ 108418, 224286-7); *Rhacophorus moltrechti* (UMMZ 199779, 201298); *Kassina senegalensis* (UMMZ 151702, 210193); *Oreophrynella quelchii* (UMMZ 85141); *Melanophryniscus stelzneri* (UMMZ 166804); *Brachycephalus ephippium* (UMMZ 103568); *Dendrophryniscus brevipollicatus* (UMMZ 204307).

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